THE BIOLOGY OF SCORPIONS¹

BY

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(With a plate and 17 figures)

INTRODUCTION

Scorpions are arthropods celebrated in both history and legend, and there is no lack of material for those seeking the reasons for their wide reputation for supernatural powers and their significance in painting and sculpture. Biologists, and palaeontologists too, can find much to interest them in scorpions. It is impossible to discuss here all the features which make them so fascinating; the present article is restricted to certain peculiar features of their biology and morphology, and attempts to explain some of the apparent contradictions which are found.

Scorpions and the related spiders belong to a group of arthropods that has been distinct for several hundred million years. Scorpions differ in many ways from insects, the whole head and thorax forming a single unit, the cephalothorax, covered by a shield. Behind the cephalothorax come an abdomen of seven segments and a tail with five, terminating in a further segment, the poison gland.

In front of the head there are two small pincer-like appendages pointing forwards; these are the chelicerae (figures 5, 8). There are

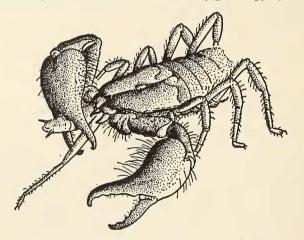


Fig. 8. Heterometrus scaber (Thorell) feeding.

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We are indebted to Dr. A. P. Mathew for the notes which appear within square brackets in the text. Also for kindly supervising the preparation of some of the figures, and supplying text figure 17—EDS.

five pairs of legs, the first pair of which, the pedipalpi, are strong and terminate in claws. The bases of these two legs form part of the mouth (figure 13). The remaining four pairs are alike, and are used for locomotion.

Behind the legs and covering the ventral part of the cephalothorax, i.e., at the start of the abdomen and behind the genital region (figure 13), there are a pair of curious appendages, the pectines or combs.

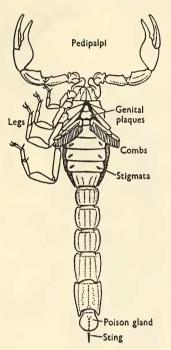


Fig. 13. Androctonus australis (L.), female. Ventral surface, showing the parts of the body. Total length 8 cm.

These are peculiar to the scorpions, and are found in both young and old of both sexes. With the poison gland, they serve to distinguish scorpions from all other arthropods.

A rare anomaly, which has attracted much attention, consists in a doubling of the tail. Figure 1 shows an adult female with two identical tails, each perfectly formed. This division of the rear end of the body sometimes also affects a portion of the abdomen; it originates during embryonic development, a case of incomplete twinning. The anomaly was known in antiquity, for Pliny, citing Aelian, placed these double-tailed scorpions in a class by themselves.

SCORPIONS AS LIVING FOSSILS

Scorpions are one of the oldest forms of life still to be found on the surface of the earth. Only a few hundred fossilized specimens are known, but it must be remembered that we are dealing with a land animal whose chances of fossilization may well have been slight. Examples recorded from many parts of the world show us that the scorpions have remained essentially unchanged for hundreds of millions

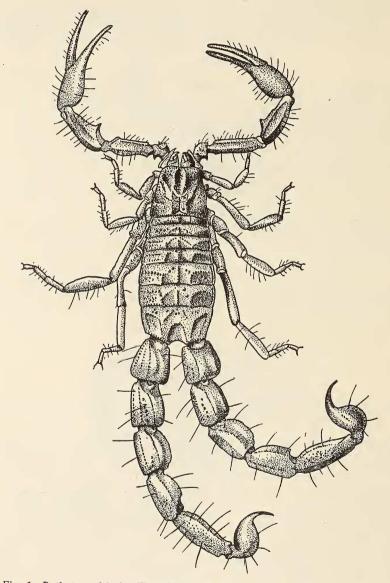


Fig. 1. Buthotus alticola (Pocock), adult female from Afghanistan, with two perfect tails. Length of body 9 cm. (After Gaillard).

of years. Fossil scorpions resemble the present-day *Pandinus* (figure 4) in possessing a pair of chelicerae, a pair of pedipalpi, four pairs of legs for locomotion, a poison gland, and ventral pectines. It is

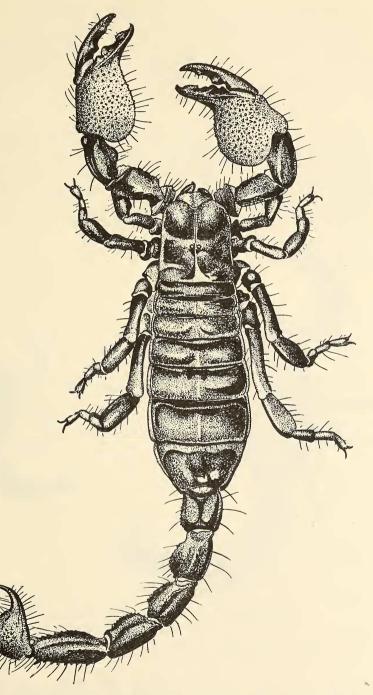


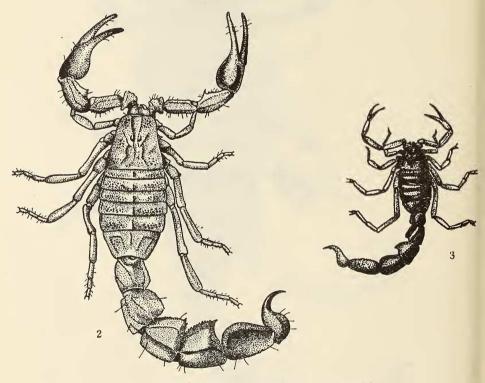
Fig. 4. Pandinus imperator (C. L. Koch), adult female from French Guinea. Length of body 18-20 cm. (After Gaillard).

thus impossible wrongly to classify a fossil scorpion, and modern scorpions may well be described as 'living fossils'.

It must not be assumed, however, that the scorpions have remained completely unchanged from the earliest times. It is possible to discern differences of detail between fossil and present-day scorpions which have resulted from an evolutionary process; these have been studied by the American arachnologist A. Petrunkevitch (5, 6).

THE STABILITY OF THE SCORPIONS

During vast epochs of time, scorpions have been subjected, like other forms of life, to great geological and climatic changes. How have they been able to resist these changes, to adapt themselves to them, and to survive? I have recently published a revision of the north African scorpions (9), of which two examples (figures 2 and 3) are shown here, and in the course of this study I have put forward certain hypotheses to explain their sustained success.



Two characteristic scorpions from north Africa

Fig. 2. Androctonus australis (L.) hector C. L. Koch, a lethal species from the northern borders of the Sahara. Length of body 9.5 cm. (After Gaillard). Fig. 3. Orthochirus innesi E. Simon, a species from the Saharan oases. Length

of body 3 cm. (After Gaillard).

North Africa has not always been a desert as it mainly is today; in the course of time it has undergone a succession of wet and dry periods. After the final rainy period of the Quaternary, a long dry

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period set in which transformed a region of luxuriant growth into a desert. How did the Tertiary fauna withstand this catastrophe? The present distribution of the scorpions of the Sahara is characteristic: they are few in numbers and are split up into small colonies, last relics of a past greatness. There are regions virtually devoid of water where scorpions, like most other animals, have completely disappeared; there remain, however, large or small regions, from mountains to oases, where conditions, though much changed, still permit life to continue. Moreover, scorpions live in the soil, under stones, or in burrows, and they can thus relatively easily find surroundings which fulfil their requirements and which are to some extent stabilized. Finally, it must not be forgotten that even large changes in the general climate are much diminished in the superficial layers of the soil. Extensive researches into microecology, especially that of insects, indicate that the micro-climate in the layer beneath the surface is largely independent of the external general climate.

Scorpions have thus managed to survive in conditions of heat and drought, first because of their subterranean habitat, and secondly because there remain here and there areas where their old conditions of life still obtain. Above all, however, they have survived because of their ecological plasticity.

It is generally believed that scorpions are characteristic of dry or desert regions, but I consider this to be wrong. They are but the remains of an ancient fauna, still quite abundant, which lived under quite different conditions of temperature and humidity. If they have survived, it is because of their great adaptability—their capabili-ties are great, their demands few. I cannot sustain this argument here in detail, but I can mention some remarkable experiments on the feeding and respiration of scorpions. They can, for example, remain in an inert condition at freezing point for a period of weeks, and yet return in a few hours to a normal mode of life. They can withstand, without hurt, total immersion in water for days on end, or the blocking of seven out of their eight lungs (4). They have remarkable possibilities of haemopoiesis (i.e., making blood) and a very small respiratory coefficient. Moreover, they are sluggish creatures and thus consume little energy in moving about. More important still, they can gorge themselves with food in a few hours, or survive without feeding for many months, even for more than a year. In my opinion, scorpions are a striking example of creatures whose persistence derives not from the fact that their surroundings have remained unaltered, but from the fact that they are able to neutralize large changes in their surroundings by resorting to their subterranean habitat; in addition, their remarkable physiology enables them greatly to vary the tempo of their existence. Largely unaffected by extremes, they are virtually independent of their surroundings; herein lies the most certain guarantee of the immortality of their race.

DETECTION AND CAPTURE OF PREY

The food of the scorpion consists of living creatures of many kinds that share its habitat, insects (both adults and larvae), spiders, millepedes, and even small rodents. The mode of capture of prey

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has often been observed, and descriptions by early naturalists are well known. Here I illustrate certain characteristic attitudes. At rest, or 'sleeping' (figure 5), the scorpion is motionless, with its ventral

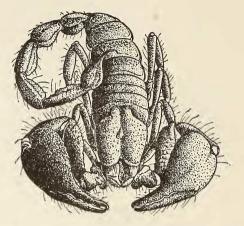


Fig. 5. Heterometrus scaber (Thorell) the large black scorpion of the West Coast of India. Length of body 13 cm. Posture at rest.

surface against the ground, the tail curved on the flat, and the legs folded. When hungry, or if a victim is detected, the attitude of the animal changes (figure 6); it moves slowly forward, supported on its

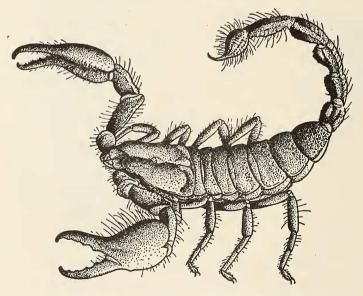


Fig. 6. Heterometrus scaber (Thorell). Posture when on defensive or in search of prey.

hind legs, with claws open and extended and tail raised and pointing forwards. Often the scorpion will then hesitate, and the final act of capture seems almost accidental, an act of defence rather than of attack. If the prey is active, the scorpion may even withdraw for a time, but it waits patiently and finally achieves its aim. Then, especially if the victim struggles, it inserts its sting (figure 7) where

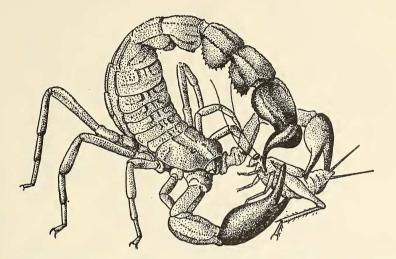
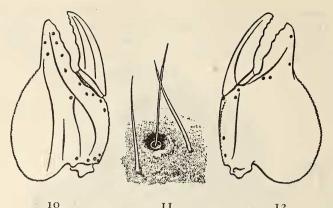


Fig. 7. Androctonus australis (L.) hector C. L. Koch, capturing and stinging prey.

best it can, often without any delay, and the prey, held in the claws, is carried towards the chelicerae. These seize it and inflict deep wounds, through which the contents of the victim's body escape and pass into the scorpion's mouth. The chelicerae play the most important part in this operation. They break down the tissues of the victim, of which there finally remains nothing but a mass of unabsorbable residues; these are sometimes got rid of by using the claws as toothpicks.

It is not entirely clear how the scorpion first detects its prey. The eyes are too crude to be of much assistance, and in any case the scorpion is a nocturnal animal for which visual impressions can be of no great significance. Other sensitive organs must therefore be concerned, notably the sensory hairs or trichobothria found only on the pedipalpi. These hairs are present at birth, and do not alter in number or position during growth. They are of considerable importance in classification (figures 10, 12), and certainly represent very primitive characters. The trichobothria are easily recognizable by the shape of their point of insertion, which resembles the top of a well (figure 11), by their fineness, and by the thinness of the membrane which links them to the integument. They are richly supplied with nerves, and can certainly detect minute air-currents such as those caused by movements of the prey. They are, in fact, like tiny receiving-sets, pointing in all directions and spaced out along the pedipalpi, which when extended act as huge antennae.



10 II I2 Fig. 10. Claw of *Scorpio maurus* (L.), a scorpion from north Africa, living in a burrow. External view, showing the sensory hairs. Fig. 11. Sensory hair, much enlarged, between two ordinary hairs. Fig. 12. Same claw as in figure 10 (internal view).

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EXTERNAL DIGESTION

The scorpion has to macerate its prey, because the mouth is able to take in liquids only. There is a powerful pharynx, which sucks the liquid contents of the victim into the large middle intestine, where it can be digested. Scorpions are not peculiar in sucking their prey, but are unusual in that digestion is effected outside the body by means of powerful enzymes ejected periodically during feeding; in this they resemble some other arachnids. As the scorpion feeds, from time to time it ceases to suck and liquid is regurgitated upon the victim. It appears that this liquid originates in the middle intestine, which is rich in glandular tissue, and that the scorpion actually regurgitates its digestive fluid during its meal. The study of external digestion in other arachnids, particularly spiders and pseudoscorpions, leads to the belief that the breaking-down of the tissues of the victim is caused not only by this intestinal fluid but by secretions form, specialized glands, analogous to salivary glands, which are poured into or over the victim at the moment of regurgitation. The anatomy of the scorpion is not sufficiently well known for this analogy with other arachnids to be perfectly reliable, but it does seem that the regurgitated fluid is activated by other substances secreted from the specialized glands, and sometimes, as in certain spiders, by the poison itself. I have recently pointed out (8) that the poison must not be considered solely in connection with the capture of prey: it is related to the feeding-process as a whole and forms but a part, albeit the best known, of the physiological complex which constitutes the external digestion. In scorpions, too, the poison has its role in this complex; it not only cuts short the victim's resistance but aids, by catalytic or other chemical action, in the digestive process itself.

REPRODUCTION AND NUTRITION OF THE EMBRYO

In scorpions the sexes are distinct, though they resemble each other in all but small details. Fertilization necessitates the coming

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The Rock Scorpion (Buthus sp.) with young on her back.

Scorpions bring forth living young. As soon as they are born they clamber on the mother's back and remain there till able to shift for themselves. The mother's 'tail' with its poison sting gives sure protection to the defenceless family.

Photo: 0. C. Edwards

together of the two sexes and is accompanied by curious display. Maccary (2) and Fabre (1) have described some of these displays, the *promenades à deux* in which male and female walk 'hand-in-hand'; and the *arbre droit* in which the two animals appear to be fighting (figure 9). The conclusion of these nuptial dances I have not observed,

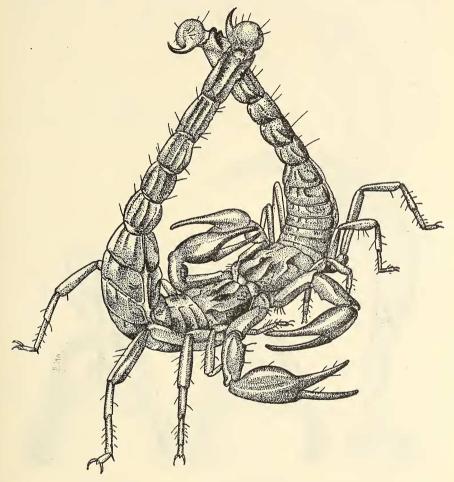


Fig. 9. Posture known as the 'arbre droit' (after Fabre, and from personal observations) preceding copulation in Buthus occitanus (Am.), a scorpion from Languedoc, France. The female is on the left.

but anatomical investigation bears out the statements of early writers; the male fertilizes the female directly in a true copulation, which is rather rare in other arachnids. In the course of this act, the male protrudes certain special organs to form a temporary penis, with which he inserts the sperm and finally places in position a vaginal plug, a kind of post-nuptial hymen (9, pp. 31-6).

The course of development of the fertilized eggs inside the mother differs according to whether the eggs are rich in yolk (as in the